THE LIFE CYCLE OF A HOMOSPOROUS PTERIDOPHYTE.

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The Homosporous Pteridophytes constitute the lowest subkingdom of vascular plants. They and all plants above them have a true fibro-vascular system and true leaves and roots in the sporophyte generation except in a few cases where leaves or roots have been lost through an adaptation to some peculiar environment. No plants below the Homosporous Pteridophytes possess true leaves, roots, or vascular system. These plants are called homosporous because in them there is only one kind of nonsexual spores produced while the three higher subkingdoms of vascular plants have two kinds of nonsexual spores and are thus called heterosporous.

The known fossil record of Homosporous Pteridophytes does not extend below the Silurian Period although they must certainly have flourished in previous geological times. They were exceedingly abundant in the Devonian and Carboniferous and were among the important coal forming plants. Many were of the tree type while at present they are mostly low geophilous perennials, although in tropical countries tree ferns are still quite abundant.

There are about 2,800 known living species of Homosporous Pteridophytes. They fall naturally into three distinct classes—ferns or Filices with 2,600 species, horsetails or Equiseteae with 25 species, and lycopods or Lycopodieae with 155 species.

The ferns are divided into two distinct subclasses called the Eusporangiatae and Leptosporangiatae. The eusporangiate ferns have the spore bearing tissue of the sporangium developed from hypodermal cells while in the leptosporangiate forms the sporangia arise from epidermal cells. The other Homosporous Pteridophytes are eusporangiate. The leptosporangiate ferns appear after the Paleozoic Era and are at present by far the most abundant. There are two orders of Eusporangiatae, the Ophioglossales and Marattiales. Some authors have attempted to associate the Ophioglossales with the Lycopods, but from a consideration of all their characteristics it does not appear that there is any evident relationship. The Leptosporangiatae are a

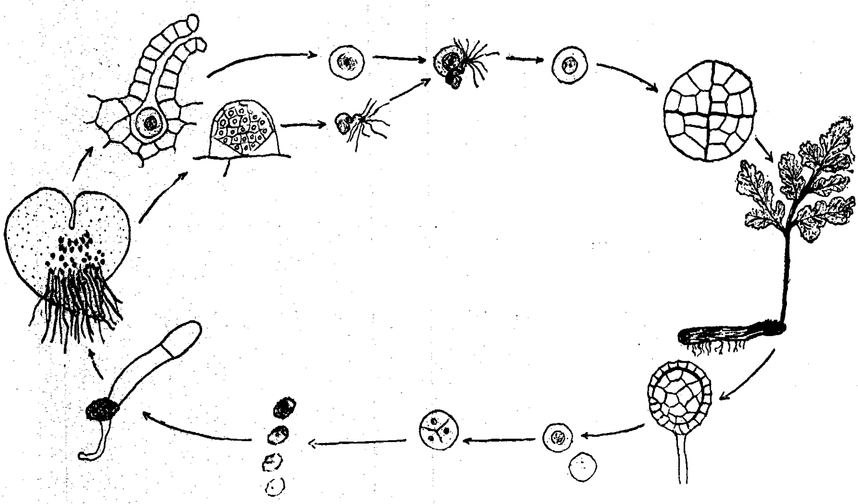

Fig. 1. Diagram of Life Cycle of Ordinary Fern.

compact group consisting of but one order, the Filicales. The ferns usually bear large, much compounded leaves but occasionally the leaves are simple and entire.

The horsetails are rush-like geophilous perennials with jointed, mostly, hollow, simple or branched, aerial stems and leaves reduced to toothed sheaths at the nodes. Some are highly impregnated with silica and are hence called scouring rushes. They are closely related and constitute but a single order, the Equisetales, with a single family and genus.

The lycopods are small herbaceous often geophilous plants with numerous small scale-like, lanceolate or subulate, simple leaves. There is but one order, the Lycopodiales, consisting of two families.

There is considerable similarity in the life cycles of the three classes. The general account given below of the life history of a leptosporangiate fern will hold good for any of our common species of Adiantum, Asplenium, or Dryopteris, but other groups may show important differences in details. In no subkingdom is the antithetic alternation of generations more clearly marked and each generation lives independently for a part of its life. The sporophyte or nonsexual generation is the conspicuous plant although the gametophyte is usually of some size and easily distinguishable except in the Ophioglossales and some Lycopodiales where it is entirely subterranean.

The sporophyte of our common ferns has a horizontal rhizome and compound leaves which commonly form a rosette above ground. The stem consists of a general ground tissue containing closed concentric fibro-vascular bundles. The stem and root tips have definite apical cells. In the Ophioglossales the bundles are open and arranged as in the higher plants, forming a ring of wood and central pith. There is also a definite cambium layer outside of the xylem cylinder.

The younger leaves of the ferns are sterile but later rosettes of spore-bearing leaves are produced. The rosette of sporophylls corresponds to the fertile or spore-bearing parts of a flower in the higher plants. In some of the lycopods there are also simple zones of spore-bearing leaves alternating with the zones of sterile foliage leaves, the growth of the stem not being stopped when the sporophylls are developed. But in other lycopods and in the horsetails the sporophylls are arranged in closely crowded cones which terminate the branches, their growth in length being permanently checked. In these groups, therefore, we have true primitive flowers—modified and specialized spore-bearing shoots. The three essentials of a flower are (1) a stopping of the growth of the floral axis, (2) a shortening of the floral axis and consequent crowding of the floral organs, and (3) a modification of the spore-bearing leaves into specialized sporophylls.

The sporangia are produced in clusters called sori, often very numerous. Each sporangium produces a number of cells which become free and more or less spherical in the sporangial cavity. These cells are called sporocytes. Each sporocyte divides twice, producing a tetrad of cells. These four cells finally separate and give rise to four nonsexual spores. During the first division in the formation of the spore-tetrad the number of chromosomes in the nucleus is reduced one-half, or from a $2x$ number to an x number. The x number of chromosomes is continued through the entire subsequent history of the following gametophyte generation. The sporangia are stalked and are provided with a peculiar ring of cells by whose contraction the cavity of the sporangium is torn open on one side and the spores thrown out.

When the spore germinates it gives rise to a short filament or protonema from the end of which a flat dorsiventral more or less heart-shaped thallus develops. The development of the gametophyte therefore falls normally into two distinct stages. In the first the plant body is a linear aggregate, in the second it is a solid aggregate. The thallus is supplied with abundant chlorophyll and is attached to the earth by means of numerous unicellular rhizoids. The thallus is hermaphrodite and develops a number of antheridia or spermaries and archegonia or ovaries on the lower side. These organs are partly imbedded in the tissues of the thallus. A number of large spirally coiled, multiciliate spermatozoids are developed in each antheridium. These finally escape, when the thallus is covered with water, through a rupture in the outer part of the antheridial wall and after swimming around for a while enter the necks of the archegonia. The spermatozoids of the horsetails are also spirally coiled and multiciliate but those of the lycopods are small and biciliate. A single oosphere or egg is produced in each archegonium. The mother cell of the egg divides giving rise to the incipient egg and the ventral canal cell. The ventral canal cell and the cells in the neck of the archegonium dissolve and at the same time the cells at the end of the neck of the archegonium, the so called lid cells, separate leaving a passage from the outside down to the egg. A spermatozoid passes down the neck to the egg and conjugates with it. This is fertilization, and during the union of the two cells their nuclei also unite, thus doubling the amount of chromatin in the cell. The fertilized egg or oospore, therefore, contains potentially $2x$ chromosomes which appear when germination takes place.

The egg germinates in the venter of the archegonium. First there is a diagonal or nearly vertical division into two cells and these each divide again, more or less at right angles to the first division, giving rise to the first four cells which are the incepts of the four regions present in the developing sporophyte embryo. One cell gives rise to the root tip, the second to the nourishing foot, the third to the stem tip, and the fourth to the first leaf. The developing embryo is entirely parasitic on the parent gametophyte which continues to manufacture food for a considerable length of time. Finally the embryo breaks through the wall of the enlarged venter of the archegonium and the root tip grows downward into the ground while the first leaf grows upward toward the light. Thus the pteridophyte embryo always passes through a bryophyte stage. The embryo passes gradually from a parasitic life and becomes completely independent when the gametophyte dies. When normal conditions are present the development of the embryo always results in the death of the parent gametophyte.

During the juvenile stage the young sporophyte usually has a type of leaves different from those of the mature condition, but gradually it becomer more and more like the mature fern and finally takes on the form normal to the species, in which condition it may live to an indefinite age. The horizontal rhizome continues to develop and branch at the tip and if decay takes place at the back end vegetative propagation is accomplished and the result is a larger and larger number of independent individuals.

The four main stages of a fern are therefore as follows:

1. The sporophyte or fern plant proper.
2. The nonsexual spores produced as the result of a reduction division.
3. The gametophyte or thallus plant.
4. The oospore produced as the result of the conjugation of the egg and sperm.

An interesting deviation from the usual type of alternation of generations is present in some ferns. In a few species a thallus may develop by vegetative propagation from the tissues of the sporophyte. This is called apospory. Or the sporophyte may develop directly from the tissues of the gametophyte and not from an egg. This is known as apogamy. The details of apogamous and aposporous structures have not been investigated to any great extent and there is still doubt as to whether or not a conjugation or a reduction takes place.

But if these important processes are omitted the change from gametophytic to sporophytic characters or vice versa may be explained in the following manner. It is evident that every cell in the gametophyte, or at the least the reproductive ones, must also contain the hereditary characters which are present in the sporophyte; but these characters are for the time being dormant. In the same way every cell in the sporophyte must also possess the hereditary characters peculiar to the gametophyte. Now, in ordinary cases gametophytic characters become active and assert themselves only as the result of a reduction division and sporophytic hereditary tendencies are only apparent after the conjugation of the egg and sperm. But there may be other stimuli able to induce the change, a response to which in the case of apogamy causes the gametophytic hereditary tendencies to become dormant and the sporophytic tendencies to become active, thus producing a sporophytic shoot; or in apospory, causes the sporophytic tendencies to become dormant while the gametophytic tendencies resume activity.

There is a difficulty in regard to the probable influence of the x and $2x$ number of chromosomes in determining the gametophyte and sporophyte generations, but the double or half number of chromosomes may not be the important factor in determining the generation. The solution of the problem must rest until the cytology of the tissues involved has been thoroughly established. However these phenomena may be explained, they must be regarded as only incidental deviations which have arisen in plants belonging to a highly specialized group originally possessing a typical alternation. The presence of apogamy and apospory has nothing to do with the normal evolution of the alternation of generations in the higher plants.